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BOTANICAL GAZETTE

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DIOON SPINULOSUM [1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 131

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(WITH SEVEN FIGURES)

Three well-defined species of Dioon have been found in the Mexican tropics: *D. edule* Lindl., *D. spinulosum* Dyer, and *D. Purpusii* Rose. *D. edule*, which was described as early as 1843, is now quite well known. Although *D. Purpusii* was described only a few months ago, the species had often been seen, but had been mistaken for *D. edule*, which it resembles in its general appearance. I was told by a Mexican botanist that I should find *D. edule* along the Mexican Southern R. R. in the neighborhood of Santa Catarina, State of Oaxaca. He said there was no other cycad in that region. The plant was easily found, and I at once saw that it was a new species intermediate between *D. spinulosum* and *D. edule*. The plant called *D. edule* in *fig. 101* of WIELAND'S *American fossil cycads* is the new *D. Purpusii*, as plainly indicated by the staminate cone and by the leaves. MACDOUGAL and ROSE collected cones of the new species in 1906 in the Tomellin cañon, where it was well shaded by bushes and small trees. PURPUS in 1908 collected seeds and bracts in the Sierra Mixteca, Puebla. In April of the same year I saw the species at various places between Santa Catarina and Tomellin, growing in dry, exposed situations, associated with cacti and Beaucarnea. ROSE[2] describes the staminate sporophylls as "bracts with recurved ovate tips," apparently supposing that the sporangia were borne on the

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[2] ROSE, J. N., Studies of Mexican and Central American plants. Contrib. U. S. Nat. Herb. 12:259–302. 1909.

adaxial surface, but of course they are on the under surface and the tips point up instead of down. His description of "seeds about 4^{cm} in diameter" needs confirmation; 4^{cm} in length would be more probable.

In general habit, in the straight, stiff, ascending leaves, *D. Purpusii* resembles *D. edule*, and the leaflets have the texture of those of *D. edule*, but they retain in some degree the spinulose character of those of *D. spinulosum*. In the number of sporangia on a microsporophyll, *D. Purpusii* is intermediate between *D. spinulosum* and *D. edule*. The ovulate sporophyll is rather slender and tapers gradually to a point, in this feature resembling *D. edule* and differing decidedly from *D. spinulosum*.

Dioon spinulosum Dyer was described by EICHLER[3] in 1883, the description being based upon a few leaves and a few trunks without leaves. Since the largest leaf was only 65^{cm} in length, the plants must have been very small. One of the trunks received by EICHLER produced a leaf which his figure shows to be that of a plant only a few years old. The material came from a nursery in Cordoba, State of Vera Cruz, Mexico, and, according to the gardener, the plants grew wild in the neighborhood of Tuxtla. The striking feature is the spinulose leaf. No cones were found, and so EICHLER remarks that it might seem doubtful whether the plant is really a Dioon ("Es möchte daher zweifelhaft erscheinen, ob die Pflanze wirklich ein Dioon ist").

DYER obtained a leaf from Yucatan, and since the locality was given as Progreso, the leaf probably came from a cultivated specimen. EICHLER agreed that DYER should describe the new species. The description, based upon the single leaf, is as follows:[4]

Folia breviter petiolata, elongato-lanceolata, rigida, plana, pinnatisecta, ad 3 pedes longa; segmentis circiter 70 utroque latere, mediis majoribus subopposita lineari-lanceolatis breviter acuminatis 18–23-nerviis, ad 4 pollices longis media latitudine semipollicaribus, basi angustiore, utroque latere spinulis pungentibus basim versus integerrimis, inferioribus in dentes palmatifidos desinentibus. *Strobili*. . . . . South Mexico, Tuxtla; Yucatan, Progreso. (C. J. Hoge). Herb. Kew.

3 EICHLER, A. W., Ein neues Dioon. Gartenflora 2:411–413. 1883.

4 DYER, W. T. THISTLETON, Cycadaceae, in Biologia Centrali-Americana Botany 3:190–195. 1882–1886.

During my second trip to Mexico, in 1906, I saw small specimens of *Dioon spinulosum* in the park at Vera Cruz, but did not find it growing wild. Gov. TEODORE A. DEHESA, of the State of Vera Cruz, who has repeatedly assisted me in my investigation of Mexican cycads, again used his influence in my behalf, and I am also under renewed obligations to Mr. ALEXANDER M. GAW, of the State Bureau of Information, Jalapa, Mexico, for his continued interest and active cooperation both in securing material and often in furnishing field notes.

Mr. GAW found that the plants in the park at Vera Cruz came from Tlacotalpam, a town southeast of Vera Cruz, and he also found that most people do not distinguish the two species, *D. edule* and *D. spinulosum*, for he was told that the plants in the park at Vera Cruz could be found growing wild in the vicinity of Tlacotalpam, Catemaco, and elsewhere in the canton of Tuxtlas, and between Palmar and Colorado on the Interoceanic R. R. Doubtless the information in regard to the first three places was correct, but since I had found only *D. edule* in the Palmar-Colorado region, Mr. GAW sent a man through that entire district with a leaf of *D. spinulosum* as a guide. The man found *D. edule* in abundance, but failed to find a single specimen of *D. spinulosum*. In Vera Cruz the plant is called *palma de Dolores*, the same name which in the Jalapa region is applied to *D. edule*. The name *tio tamal*, which is commonly given to *D. edule* because the seeds are used in making *tamales*, does not seem to be applied to *D. spinulosum*, although its seeds are edible. The natives of the coast region call both the plant and the seeds *chicalitos*, a name which I have not heard applied to *D. edule*.

From a park in Tlacotalpam Mr. GAW secured a large ovulate cone of *D. spinulosum*, and he was told that the specimen came from the Sierra de Oaxaca Mountains near Tuxtepec, where the plant was said to be very abundant. As the Tlacotalpam cone had only abortive seeds, Mr. GAW, after repeated efforts, succeeded in securing from the Tuxtepec region an ovulate cone in which pollination and fertilization had taken place. Later he secured a cone with ripe seeds, which germinated readily. With the material Mr. GAW sent the rather startling information that, according to the natives, the cones are borne below the crown of leaves and not above the crown, as in *D. edule*.

In March 1908 I visited southern Mexico to collect *D. spinulosum*. While on the way to Tuxtepec, I was informed that a plant which seemed to agree with my description, except that it was much taller, could be found near Tierra Blanca. In the mountains west and a little north of Tierra Blanca I found a few specimens and was told that plants were more numerous a few miles farther south. The information was correct, for on the immense hacienda of the Joliet Tropical Plantation Company, a short distance from Tierra Blanca and about 60 miles south of Vera Cruz, magnificent specimens are abundant. Mr. J. C. DENNIS, superintendent of the plantation, very generously furnished horses, guides, and the hospitality of his palatial home while I explored the mountains and secured photographs and material. The plant is usually well shaded, growing among the prevailing limestone rocks which have given name (Tierra Blanca) to the region.

From Tuxtepec, a town on the Papaloapam River about forty miles southwest of Tierra Blanca, half a day's ride on horseback brings one to the mountains where *D. spinulosum* is as abundant as at Tierra Blanca. In some places it is the only large plant, and it would not be an exaggeration to speak of a Dioon forest. Beautiful specimens, which might have been the pride of any conservatory, had been cut down to get the cones, because it was easier to cut the tree than to climb it. The natives use the young seeds in making *tamales*, as in *D. edule*, and at a later stage the dry stony seed coat is a common plaything for children. At Tuxtepec the dry seeds, each pierced with two holes, sell for fifteen cents a dozen. The Indians said that the plant extends some distance farther south, but that it does not occur on the western (Oaxaca) side of the mountains.

Dioon spinulosum, with the exception of the Australian *Cycas media*, is the tallest cycad known, and its slender trunk with a large crown of leaves gives it the appearance of a palm (*fig. 1*). I measured specimens 12^m in height, and Drs. BARNES and LAND, visiting the Tierra Blanca region a few months after my return, found specimens more than 16^m in height, almost as high as the tallest known specimens of *Cycas media*. The slender trunk and graceful curve of leaves are in striking contrast with the stocky trunk and straight, rigid, ascending leaves of *D. edule*.

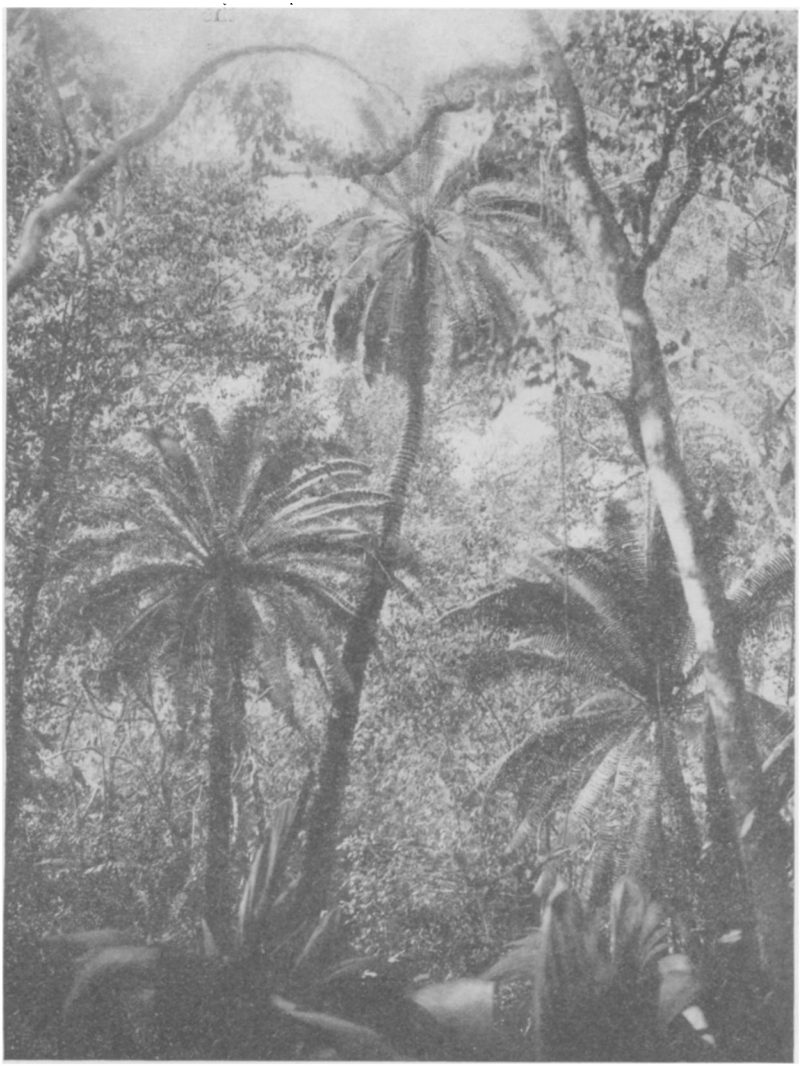

FIG. 1.—*Dioon spinulosum* on the Hacienda de Joliet near Tierra Blanca, March 1908; the tallest plant is about 10^m in height.

The ribbed surface of the trunk is due to successive crowns, and affords some basis for an estimate of the age of the plant, but in the lower part of the trunk of tall specimens the ribs may become too obscure for accurate counting. The scars of the individual leaves, which are so distinct in *D. edule*, are so obscure in *D. spinulosum* that counting in the lower portion of large trunks is out of the question. Whether the duration of the crown is two years, as in *D. edule*, I was not able to determine, but assuming the duration to be two years, the tallest specimens might not be more than 400 years old. However, any estimate can be little more than a guess, until the duration of crowns, and the effect of scale leaves, cones, and resting periods upon the growth of the trunk have been studied much more carefully. Still, I am inclined to believe that a 10^{m} specimen is no older than a 1^{m} specimen of *D. edule*.

At the base the trunk is much enlarged, often having twice as great a diameter as it has 0.5^{m} higher up. The roots are often exposed for considerable distances, especially in precipitous places, where a root may hang down along the surface of the rock. One root hanging down in this way was exposed for a distance of more than 12^{m} and was 5^{cm} in diameter where it again entered the soil.

Cutting through the trunk, which is not nearly so hard as that of *D. edule*, it is seen that there is a single zone of wood surrounding the large pith. The origin and development of the vascular cylinder, as seen in embryos and young seedlings, is being studied by HELEN A. DORETY.

Both EICHLER and DYER gave accurate descriptions of the leaves as they appear on small plants. EICHLER'S largest leaf (65^{cm} in length) had 38 pinnae, the lowest of which were rudimentary. DYER'S leaf was about 1^{m} long, with 70 pinnae on each side. On plants 2^{m} or more in height the leaves reach their full size, so that leaves 2^{m} long, with 100 leaflets on each side, are not uncommon, while one leaf measured 2.2^{m} in length and had 117 leaflets on each side, the leaflets being 20^{cm} long and 10^{mm} wide. There is great variation in the leaflets, some only 14–15^{cm} long being 15^{mm} wide. There are 5–8 sharp spines on each margin of the leaflets of large leaves. The lower leaflets become more and more reduced, until the lowest ones are nothing but spines, so that the leaf bears considerable resemblance

to that of Encephalartos. The leaves of seedlings have comparatively few leaflets, the first leaf sometimes having less than a dozen on each side. It is interesting to note that in seedlings the leaves have no reduced leaflets, even the lowest being as perfectly formed as those in the middle of the leaf. The leaflets of seedlings have fewer spines than those of older plants, there being only 2–6 on each margin. The midrib is not so large as in *D. edule* and the leaves are much thinner. A few leaflets of a leaf of medium size are shown in *fig. 2*.

Remembering that the natives had reported cones growing below the crowns, one would naturally think of the condition in Bennettitales.

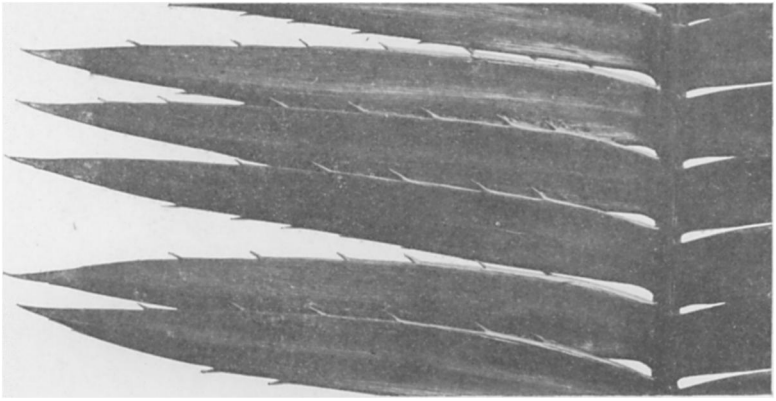

FIG. 2.—Portion of leaf of *Dioon spinulosum* from a specimen at Tlacotalpam; $\times\frac{3}{4}$; the cone shown in *fig. 4* came from the same plant.

A glance at *fig. 3* will show that the cone does hang down below the crown. An examination of the apex of the stem shows, however, that the cone is borne in the center of the crown as in *D. edule*, but that a considerable elongation of the peduncle, together with the great weight of the cone, causes the cone to bend over, slip between the leaves, and thus hang below the crown. Consequently no seeds are found in the nest of the crown as is so commonly the case in *D. edule*, where the germination of seeds in this position often gives rise to the appearance of branching. In *D. spinulosum* branching is rare. Seedlings are found for a considerable distance around the large ovulate plants. The natives say that at maturity the cone bursts with a loud noise, scattering the seeds, or *coyoles*, the plant being called *coyolillo*.

FIG. 3.—*Dioon spinulosum* with ovulate cone, on the Hacienda de Joliet, March 1908.

The ovulate cone is the largest yet known for any gymnosperm. In March, cones weighing 14 kilos were not infrequent, and occasionally a cone had reached a weight of 15 kilos. Since the seeds are not fully mature until October, it is safe to assume that the cones increase somewhat in weight after March, the time of my visit. The cone is cylindrical ovoid (*fig. 4*), its general habit distinguishing it at once from the ovoid cone of *D. edule*. It reaches a length of 50^{cm} and a diameter of 27^{cm}, but the average cone is about 20 per cent. smaller than these measurements.

FIG. 4.—*Dioon spinulosum;* ovulate cone from a cultivated plant at Tlacotalpam; $\times \frac{1}{3}$; November 1906.

The ovulate sporophylls are very hairy, as in *D. edule* and *D. Purpusii*, but are much more closely imbricated, there being no projecting tips as is always the case in the upper part of the cone of *D. edule* and probably in *D. Purpusii*. In regard to the latter species, however, my statement is based upon only a single sporophyll. The

sporophyll of *D. spinulosum* is thick, fleshy, and rounded or obtuse at the apex, contrasting again with the long tapering sporophylls of *D. edule* and *D. Purpusii*. The contour of the exposed portion of the sporophylls and the close imbrication is seen in *fig. 4*, especially near the apex of the cone.

The seeds are white and perfectly smooth, but may become slightly yellowish when mature; their length varies from 4 to 5.5^{cm} and the diameter from 2.5 to 3.5^{cm}. Some of the ovules have the

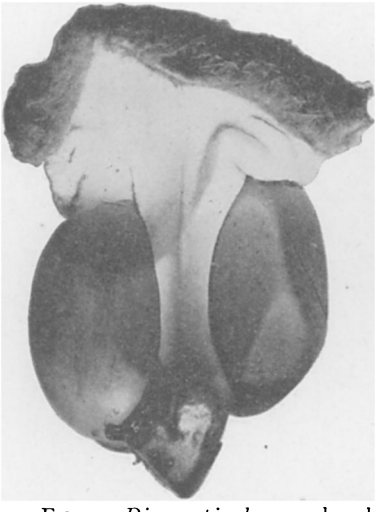

FIG. 5.—*Dioon spinulosum;* dorsal view of an ordinary sporophyll, the ovule on the left showing the false stalk; from a cone received from Tuxtepec, April 1907. $\times\frac{3}{4}$.

FIG. 6.—*Dioon spinulosum;* ovulate sporophyll, from the cone shown in *fig. 4*, with five ovules, three of which can be seen on the left side, but only a portion of one of the two on the right side is visible. $\times\frac{3}{4}$.

false stalk, characteristic of the genus, but it is not as frequent as in *D. edule* (*fig. 5*). In one cone, with only abortive ovules, there were frequently more than two ovules on a sporophyll, in some cases as many as five or six (*fig. 6*). Cycas, the most ancient genus of the family, regularly produces more than two ovules on a sporophyll, and in Dioon the production of more than two ovules is doubtless a recurrence of the ancient habit. In rare cases, I have noted as many as four ovules on the sporophylls of *Zamia floridana* and *Ceratozamia mexicana*.

As yet I have obtained only one staminate cone, and that not from the field but from Professor TRELEASE, of the Missouri Botanical Garden. Where the specimen came from could not be determined, except that it had been secured from the nursery of W. A. MANDA (S. Orange, N. J.), who had gotten it in a miscellaneous collection of unknown sources. This cone, which arrived in Chicago July 25, 1907, measured 21^{cm} in length by 10^{cm} in diameter, and since the pollen was nearly mature, this must be about the size before the elongation of the axis begins to separate the sporophylls and liberate the pollen. The general appearance of the cone is shown in *fig. 7*.

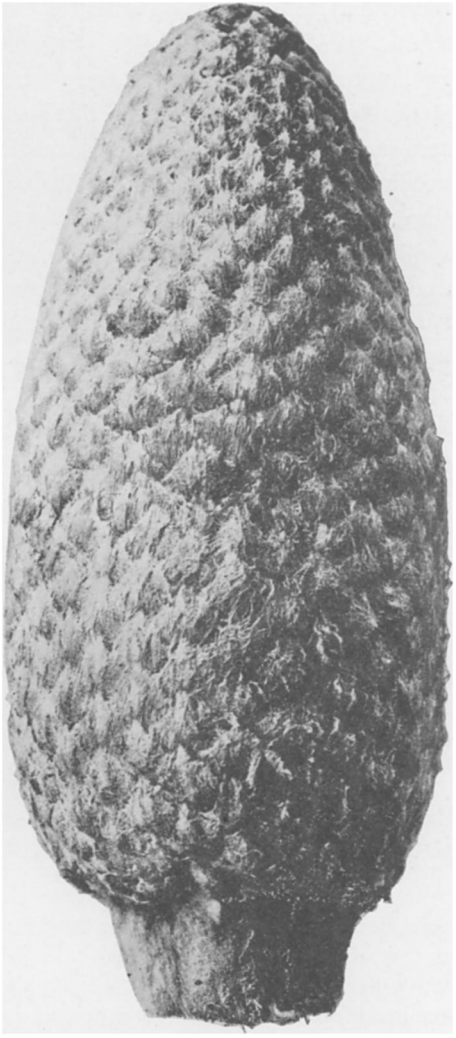

FIG. 7.—*Dioon spinulosum;* staminate cone from a plant in the Missouri Botanical Garden, July 1907. ×⅔.

The shape of the microsporophyll and its general appearance is about as in *D. edule*, except that the microsporangia are much more numerous, the average number on a microsporophyll being about 750; while in *D. edule* the average falls a little below 300. The number in *D. Purpusii* is between 300 and 400. In all three species the sporangia are in sori of 3, 4, 5, and 6 sporangia, with 4 and 5 the most frequent numbers.

While it is hardly safe to arrange the three species in an evolutionary sequence before the life histories have been studied, it seems to me that *D. spinulosum* is the oldest and *D. edule* the most recent, so that the series should be *D. spinulosum*, *D. Purpusii*, and *D. edule*. In favor of this sequence it may be said that *D. spinulosum* has a spinulose leaf throughout its life history, while *D. edule* shows the spinulose character only in the seedling, the later leaves gradually becoming entire. *D. Purpusii* has a leaf which is slightly but constantly spinulose in the adult plant. Its seedling is not known. Regarding the spinulose character of the seedling leaf of *D. edule* as due to recapitulation, *D. edule* is a later development than *D. spinulosum* and has come either from *D. spinulosum* or from some unknown form with spinulose leaves. The leaves of *D. edule* and *D. Purpusii* present about such characters as we should expect in *D. spinulosum*, if this species should be brought from its well shaded habitat into the dry hot places where the other two species are found.

I believe that throughout the Cycadales there has been a gradual reduction in the number of sporangia on a sporophyll. On this basis the sequence would be as I have given it.

On the other hand, it must be admitted that in *D. edule* the ovulate cone is not so compact and the megasporophylls have not lost so completely the character of the vegetative leaf, which must be assumed as the ancestral form of both kinds of sporophylls.

Since the original description of *D. spinulosum* was necessarily inadequate and incomplete, it seems worth while to describe the species from the more abundant material now available.

DIOON SPINULOSUM Dyer.—Adult plants 2–16^{m} in height; stem slender, with conspicuous transverse ribs, and a single zone of wood; leaves 1.5–2^{m} long, curved, with 80–117 leaflets on each side; leaflets 15–20^{cm} long, 10–15^{mm} wide, with 5–8 spines on each margin, the lower ones gradually reduced to mere spines; first leaf of seedling with as few as a dozen leaflets on each side, the leaflets with only 2–6 spines on each margin, lower leaflets not at all reduced; ovulate strobilus cylindrical ovoid, 35–50^{cm} in length, 20–27^{cm} in diameter; sporophylls densely hairy, closely imbricate, the exposed portion rounded or obtuse at apex; seeds smooth, white, 4–5.5^{cm} in length, 2.5–3.5^{cm} in diameter; staminate strobilus elongated ovoid, 21^{cm} in length, 10^{cm} in diameter; exposed portion of sporophyll hairy, obtuse; microsporangia about 750 on a sporophyll.

Observed growing wild at Tierra Blanca (State of Vera Cruz) and at Tuxtepec (State of Oaxaca), Mexico.

Material has been collected at intervals and a future account will deal with critical stages in the life history.

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